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Cascading effects of moose (*Alces alces*) management on birds

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Abstract Large herbivores often have key functions in their ecosystems, and may affect ecosystem processes with cascading effects on other animals. The mechanisms often involve relocations of resources of various kinds, including reduction in resource availability following foraging and increase in resources from animal excreta. As large herbivore populations in Europe generally are intensely managed, management activities may interact with the activities of the herbivores themselves in the effect on other ecosystem components. We investigated the effects of moose (*Alces alces*) winter browsing, together with the effect of net nutrient input via supplementary winter feeding of moose on functional composition and species richness of birds in a boreal forest. Supplementary feeding stations for moose had a net zero effect on bird species richness and abundance, because negative effects of moose browsing were balanced by positive effects of nutrient input. Sites with a similar browsing intensity as at feeding stations but without nutrient input had lower abundance and species richness than feeding stations. Functional groups of bird species showed differing responses: birds nesting at or below browsing height were negatively affected by moose browsing, whereas species nesting above the browsing zone were positively affected by moose browsing. Insect-eating species responded negatively to moose browsing on birch but positively to nutrient input at feeding stations, whereas seed-eating species responded positively to birch browsing and negatively to feeding stations. This study showed that both high levels

of cervid activity and human management interventions influence bird communities.

Keywords Bird diversity · Boreal forest · Functional group · Herbivory · Supplementary feeding

Introduction

Large herbivores often have key functions in their ecosystems (Hobbs 1996). They have the potential to directly and indirectly influence the growth and structure of individual plants and plant parts, population dynamics, composition and succession of plant and animal communities, as well as fundamental ecosystem processes like nutrient cycling (Danell et al. 2003; Hester et al. 2006; Hobbs 1996; Pastor et al. 2006; Persson et al. 2000; Skarpe and Hester 2008; Suominen et al. 2008). The high density of cervids in Europe, North America and Japan during recent decades has raised concern about how this may affect ecosystem components such as bird species diversity in temperate and boreal forests (Allombert et al. 2005; Côte et al. 2004; Fuller 2001; McShea and Rappole 2000; McShea et al. 1997; Miyashita et al. 2004). During recent decades, populations of the Fennoscandian moose (*Alces alces*) have increased to densities that have probably not been experienced in post-glacial times (Cederlund and Bergström 1996). A large herbivore such as the moose can modify the environment for other species by its selective feeding, trampling, urination and defecation (Berger et al. 2001; Melis et al. 2007; Pastor et al. 1993; Persson et al. 2000; Suominen et al. 2008). Ecosystem effects on other animals and long-term effects are poorly known (Suominen and Danell 2006), and there is a need for research on the cascading effects of high densities of cervids on different animal taxa.

Supplementary feeding is a management tool used to increase winter survival of cervids, reduce damage to forest plantations and minimise ungulate–vehicle collisions (Gundersen et al. 2004; Luccarini et al. 2006; Putman and Staines 2004; Weisberg and Bugmann

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2003). Supplementary feeding of moose with silage during winter is common in Norway, and leads to extremely high moose densities locally around feeding stations (Gundersen et al. 2004). Supplementary feeding also constitutes a local net input of nutrients directly from feed remains and indirectly via animal dung and urine. The high moose density and nutrient input may be expected to have cascading effects on the ecosystem locally around feeding stations.

High ungulate densities can affect the diversity and abundance of birds by modifying habitat structure and food resources (Fuller 2001; Suominen and Danell 2006). Moose browsing in boreal forest may lead to a reduction of deciduous trees, which are important for many bird species (Stokland 1997) and to a more open canopy (Persson et al. 2000), which may increase predation risk (Martin and Joron 2003) and reduce availability of nesting sites (Allombert et al. 2005; Berger et al. 2001; DeCalesta 1994; McShea and Rappole 2000). Some studies of moderate browsing have shown positive effects on invertebrates (Danell and Huss-Danell 1985), constituting an important food resource for many bird species, but high browsing pressure over long time-periods is usually negative for invertebrate abundance (Stewart 2001; Suominen et al. 2008). Also, seed production, which is important for seed eating birds, may respond to browsing (Bergström and Danell 1987). While moose browsing in boreal forest may reduce resource availability (Pastor and Naiman 1992; Persson et al. 2005b, 2007), supplementary feeding of moose brings resources into the system with potential positive effects on productivity. Nutrient input may affect plant production, chemistry and the way the trees respond to browsing by compensatory growth (Danell et al. 1997; Persson et al. 2007), which in turn may have effects on invertebrate fauna or seed production and hence food availability for birds. The forage provided for moose may also contain seeds or insects that contribute directly to food availability for birds.

We investigated the effects of long-term supplementary winter feeding of moose on the community of small to medium-sized birds in a boreal forest system in South-East Norway. The distribution of moose around supplementary feeding stations in winter makes it possible to study gradients in moose winter browsing and net input of nutrients. Both herbivory and nutrient input can have positive, negative or unimodal effect on species richness (Mackey and Currie 2001; Waide et al. 1999). Since moose densities around feeding stations are very high (van Beest et al. 2010), and nutrient availability in boreal forest is generally low (Bonan and Shugart 1989), we expect negative effects of moose browsing and positive effects of nutrient input on bird species richness. The aim of this study was to test how moose browsing can affect bird species richness and abundance, and if different functional groups of birds may respond differently. However, at feeding stations we may have effects of both moose browsing and input of nutrients. This leads to three possible scenarios:

1. Feeding stations have a negative effect on bird species richness and abundance, because negative effects of moose browsing are stronger than positive effects of nutrient input.
2. Feeding stations have a net zero effect on bird species richness and abundance, because negative effects of moose browsing are balanced by positive effects of nutrient input.
3. Feeding stations have a positive effect on bird species richness and abundance, because effects of nutrient input are stronger than browsing effects.

Materials and methods

Study system

This study was carried out in Stor-Elvdal municipality, Hedmark County in southeast Norway (~61°N, 11°E). The study area is situated between 291 and 684 m a.s.l. in the middle and northern boreal vegetation zone (Moen et al. 1999). The area is dominated by a main river valley running northwest–southeast, interspersed by side valleys and mountainous areas. The forest in this area consists of pure or mixed stands of Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), downy birch (*Betula pubescens*) and silver birch (*Betula pendula*), interspersed with species such as grey alder (*Alnus incana*), rowan (*Sorbus aucuparia*), aspen (*Populus tremula*) and willow (*Salix* spp.). Most of the forest is managed for commercial production of timber or pulp. The field layer vegetation is often dominated by dwarf shrubs such as cowberry (*Vaccinium vitis-idaea*) and bilberry (*V. myrtillus*). Data from weather stations in the valley bottom from the last 30-year period show a mean summer temperature of 10.6°C (May–September) and mean winter temperature of –5.8°C (October–April). During the same period, the mean annual precipitation was 628 mm and the mean snow depth 39 cm (eKlima 2008; <http://eklima.met.no/>). The bird community in the area is typical for a Scandinavian boreal forest, and is dominated by migratory species such as the chaffinch (*Fringilla coelebs*) and willow warbler (*Phylloscopus trochilus*) in summertime, and more resident species such as Eurasian siskin (*Carduelis spinus*) and tit species (*Parus* spp.) in the winter, with occasional peaks in drifting species such as crossbills (*Loxia* spp.).

The moose population in the area is mainly migratory, spending the summer at higher altitudes and migrating down to the valley bottom where the snow depth is lower in winter. The landowners have carried out organised supplementary winter feeding of moose with grass silage since 1990 (Gundersen et al. 2004), to reduce traffic accidents and damage to young pine stands. On average, around 600 (±140 SE) tonnes of silage is provided each year in Stor-Elvdal municipality, increasing over the last 10 years (Stor-Elvdal landowner

association, unpublished data). In the winter of 2006–2007, before this study was carried out, approximately 778 tonnes silage were deposited at feeding stations in the municipality. This equals an average of 63–78 kg nitrogen per feeding station. The effects of the nutrient input can be observed locally around feeding stations, by an increase in herbaceous vegetation growth and flowering and in presence of nitrogen-demanding species in the field-layer vegetation (Torgersen 2008). The feeding stations are placed mainly along forest roads in the side-valleys. The overall moose density in the municipality is about ~ 1.1 moose per km^2 (Gundersen et al. 2004), but in winter the effective moose density is many times higher in the valley bottom. In 2007, when this study was carried out, moose density at 1 km distance from feeding stations was 3.6 ± 1 moose per km^2 [estimated from pellet counts (see below)] assuming 14 pellet groups per moose per day in winter (Persson et al. 2000) and a winter period of 180 days). At a local scale of 25–50 m radius around feeding stations, pellet group density corresponded to a moose density of 130 ± 20 moose per km^2 ; however, this reflects intensive use of feeding stations by moose, rather than population density in the area.

Field procedures

We performed replicated point counts of birds at 11 supplementary feeding stations for moose and 11 control sites. Point counts are appropriate for comparisons of relative densities between habitats (Bibby et al. 2000) and feeding stations represent points of high moose density and input of nutrients in the landscape. The feeding stations used in this study had been in use for more than 10 years, thus reflecting long-term effects on the ecosystem. The control sites were selected to have similar vegetation types as the feeding stations, with similar elevation (290–680 m a.s.l.) (Table 1) and distance to forest roads, and all controls had a minimum distance of 1 km from any feeding station. All sites had a nest box for small birds that was used in a parallel study on reproduction, which might lead to a somewhat higher occurrence of hole-nesting species in this survey than is otherwise common for this type of forest. However, this was similar for feeding stations and controls.

The study was carried out between early May and mid-June 2007. Each site was visited five times during the study period, approximately once a week. All sites were visited on the same day between 04:30 and 08:30 a.m. Days with wind or heavy rain were avoided. The three to four observers and the time of day were rotated systematically among sites and sampling days to avoid bias due to observer or time of day. All observers had previous experience with observing birds, and were trained on bird species common for this region. During observation, all vocalisations of territorial males were counted for 10 min, as an indicator of the relative abundance of breeding territories. The song of bird

species that carried further than 1 km would be recorded at both feeding stations and controls, but this would not have any net effect on the comparison between feeding stations and controls. As the effects of feeding stations are quite local in scale (Gundersen et al. 2004), we expected effects on species with small home ranges, and this study was designed to detect local-scale differences in relative density.

For all sites that were used in bird counts, we recorded habitat variables in May–June as follows: moose pellet groups were counted in five circular plots of 50 m^2 , one plot at the observation point and four plots 25 m from the observation point in each of the directions north, south, west and east. Only pellet groups from the preceding winter were counted. The age of the pellet group was determined on basis of pellet colours/moisture and cover of leaf litter (Neff 1968). Moose browsing pressure was estimated as the percentage of browsed shoots of shoots available at browsing height (0.5–3 m) in the same plots. We estimated browsing pressure on trees of birch, pine and spruce separately, and other species (rowan, aspen, willow, alder) were grouped together because of their low densities. In addition, we surveyed vegetation variables in July, in a circular plot of 10 m radius around the observation point, to give a rough estimate of vegetation type, similar to the relevé method (Almendinger and DNR 2007). These variables were: percentage vertical canopy cover of trees with total height below and above 3 m for birch, pine, spruce and other species (grouped), and percentage ground cover of the categories herbs, lichens and dwarf shrubs. The sites were categorised by forest vegetation type (Moen et al. 1999): 1 lichen forest, 2, cowberry–bilberry forest, 3 heather bog–bilberry pine, 4 bilberry forest and 5 small-fern forest. The age of the forest was categorised according to Norwegian forestry cutting classes: 1 clearcut; 2 trees up to 8 m height; 3 trees higher than 8 m, but not mature; 4 forest mature for cutting; 5 old growth forest.

Statistical analyses

Comparison of habitat at controls sites and feeding stations

To ensure that control and feeding station sites were similar in vegetation type, and different in moose activity, we compared browsing, pellet group density and habitat variables between all feeding stations and controls with an ANOVA (or Kruskal–Wallis for non-normally distributed variables) using SAS software (SAS Institute 2003). Feeding stations and control sites had similar vegetation types, elevation and canopy cover of tree species, indicating that control sites were appropriate (Table 1). Birch browsing (%), spruce browsing (%), pellet groups density and percentage herb cover were significantly higher at feeding stations compared to controls, and percentage cover of dwarf shrubs was

Table 1 Comparison of habitat between feeding stations for moose ($n = 11$) and controls (> 1 km from feeding station, $n = 11$): mean and standard errors and test statistics for all habitat variables and moose activity variables

Variable	Feeding station	Control	F/X^2	P
Moose variables				
Pellet group density pr m ²	2.39 ± 0.71	0.06 ± 0.01	$F_{1,20} = 25.01$	0.0001*
Birch browsing (%)	95.08 ± 2.48	65.34 ± 8.79	$X^2_{1,20} = 8.91$	0.0028*
Pine browsing (%) ^a	90.01 ± 4.24	100 ± 0	$X^2_{1,11} = 5.12$	0.024*
Spruce browsing (%)	65.17 ± 13.05	4.6 ± 2.14	$X^2_{1,20} = 11.93$	0.0006*
Habitat variables				
Canopy cover above 3 m height (%)				
Spruce	12.64 ± 7.03	12.91 ± 2.63	$F_{1,20} = 2.21$	0.15
Birch	11.45 ± 3.84	12.18 ± 3.41	$F_{1,20} = 0.05$	0.82
Rowan/aspen/willow/alder	7.73 ± 7.23	2.09 ± 1.48	$X^2_{1,20} = 0.16$	0.68
Pine	7.18 ± 2.82	8.27 ± 3.21	$X^2_{1,20} = 0.06$	0.81
Canopy cover below 3 m height (%)				
Birch	8.18 ± 1.51	9.91 ± 3.51	$F_{1,20} = 0.21$	0.65
Spruce	4.91 ± 1.28	4.36 ± 1.18	$F_{1,20} = 0.04$	0.84
Rowan/aspen/willow/alder	4.73 ± 1.62	3.91 ± 1.36	$F_{1,20} = 0.01$	0.91
Pine	0.41 ± 0.15	1.27 ± 0.5	$X^2_{1,20} = 3.33$	0.068
Canopy cover of field-/ground layer vegetation (%)				
Dwarf shrubs	24.27 ± 6.39	59.55 ± 7.88	$X^2_{1,20} = 7.64$	0.0057*
Herbs	40.91 ± 10.18	14.82 ± 7.92	$X^2_{1,20} = 4.93$	0.027*
Lichens	14.73 ± 4.54	16.82 ± 4.04	$F_{1,20} = 0.66$	0.43
Forest type				
Cutting class	2.64 ± 0.2	3 ± 0.23	$X^2_{1,20} = 1.50$	0.47
Vegetation type	3 ± 0.43	2.64 ± 0.34	$X^2_{1,20} = 1.40$	0.50
Elevation	423 ± 26.9	431 ± 36.9	$F_{1,20} = 0.03$	0.86

For explanation of forest types, see methods

* $P < 0.05$ (significant)

^aPine browsing had very low sample size, and the variation at controls = 0, so the statistical significance probably does not reflect a biological significance, as pine was heavily browsed at all feeding stations and controls

significantly lower, indicating a higher level of moose activity at feeding stations compared to controls (Table 1). However, variation in birch browsing pressure was also high within control sites (Table 1). Pine browsing was 90–100% both at feeding stations and controls, but the sample size of plots containing pine was too small for a reliable test between feeding stations and controls.

Analysis of species richness and abundance

We tested for differences in bird species richness and abundance between feeding stations and controls with ANOVA using the average of all five replicates per station. Hypothesis testing of control versus feeding stations showed no significant differences in bird species richness or abundance. We therefore further used model selection to investigate which habitat- and methodological variables were important in explaining bird species richness and abundance, using the selection criteria AICc (corrected Akaike information criterion) (Burnham and Anderson 2002), and among models with $\Delta AICc < 2$ we selected the most parsimonious model (the model with the fewest model terms) (Quinn and Keough 2002). The minimum adequate model was then used to evaluate the effect of feeding stations on species richness and abundance.

We investigated the effects of observer, date and time of day and habitat variables on species richness and

abundance in a mixed model with repeated design (station/date) with Poisson distributed errors using the GLIMMIX macro in SAS software (SAS Institute 2003). We chose several candidate models by selecting the most relevant habitat variables (see below) and analysing several combinations of these (Table 2). The explanatory variables analysed were date, time, observer, feeding treatment (control, feeding station), percentage birch browsing, cutting class, and vegetation variables (see below). We investigated the relationship between explanatory variables with simple correlations to avoid including highly correlated variables (Graham 2003). As spruce browsing and moose pellet density were correlated strongly with feeding treatment, they were not included in the model. Pine browsing was not included in the model because of low occurrence of pine within browsing height and low variation in browsing pressure. Therefore, birch browsing was the variable that best represented the gradient in moose browsing intensity. For the categorical variables with many levels, such as date, observer and cutting class, we first did pair-wise comparisons using Scheffé corrections within the full model, to see which levels were significantly different from others, and then grouped the levels that were not significantly different, to reduce the number of parameters.

To include all the vegetation variables measured, but avoid intercorrelation, we performed a principal component analysis (PCA) of all vegetation variables (tree cover, field layer/ground cover and vegetation type), and

Table 2 Results from selection of variables in SAS in a mixed model with Poisson-distributed errors for species richness of singing males at feeding stations (FS) for moose and controls (C)

Model	Variables ^b	Parameters/Num <i>df</i>	−2 log likelihood	ΔAIC _C
1	FS_C dategr1 time obsgr2 birchbr vegpca2	10	31.4	0
2	FS_C dategr1 obsgr2 birchbr vegpca2	9	33.9	0.1
3 ^a	FS_C obsgr2 birchbr vegpca2	7	37.3	0.8
4	FS_C dategr1 time obsgr2 birchbr cc vegpca2	13	27.9	2.1
5	FS_C obsgr2 birchbr	6	41.9	3.1
6	FS_C dategr1 time obsgr2 birchbr cc vegpca1 vegpca2	14	26.9	3.7
7	FS_C date time obs birchbr vegpca2	15	24.9	6.4
8	FS_C date time obs birchbr cc vegpca2	18	21.1	9
9	FS_C date time obs birchbr cc vegpca1 vegpca2	19	19.8	10.6
10	FS_C birchbr cc vegpca1 vegpca2	8	58.7	24.5
11	FS_C birchbr cc	6	66	27.2

AIC_C Corrected Akaike information criterion

^aMinimum adequate model

^b*Birchbr* Birch browsing, *Dategr1* 5 dates grouped in 2 groups, *obsgr2* 5 observers grouped in 3 groups, *Vegpca 1 and 2* axis 1 and 2 from a PCA of vegetation parameters, *CC* forest cutting class, *time* time of day

included the sample scores of PCA axis 1 and 2 in the model. Axis 1 was correlated positively with herbs and vegetation type 5 (small-fern forest) and negatively correlated with dwarf shrubs, representing the gradient between richer vegetation types with herbs/grasses and poorer vegetation types with cowberry/bilberry woodland. Axis 2 was positively correlated with cover of spruce > 3 m high and negatively correlated with lichen cover, representing the gradient from spruce to lichen/pine forest.

For the variables such as observer, date and time of day, we first investigated if they had any effect in a linear model of species richness/abundance including all the variables. Species richness varied among observation days ($F_{4,79} = 3.27$, $P = 0.016$), but with no consistent trend in time. Species richness also varied among observers ($F_{4,62} = 6.95$, $P = 0.0001$) and time of day ($F_{1,79} = 7.84$, $P = 0.0064$). However, because observers and time of the day were systematically rotated among sites and days of observation, this did not lead to any visible bias in the results. These variables were included in further modelling, to account for the effect of observer, date and time. Total abundance of territorial males showed the same variation with time, date and observer as species richness did.

Analysis of functional groups and individual species

All bird species were grouped into functional groups (see Appendix) according to migratory strategy (migratory/resident/drifted), main feeding ecology in the observation period (insects/seeds/buds, woodpeckers forming a separate group) and nesting height (below, at and above 0.5–3 m browsing height for moose) (Cramp 1977), to see if functional groups differed in response to feeding treatment and habitat variables. Investigation of abundance of groups according to diet/migration and their relation to habitat variables was analysed by ordinations in the statistical software package Canoco (ter Braak and Smilauer 2006). Linear response models were used, as the gradient determined by the first axis of a detrended

correspondence analysis (DCA) was below four standard deviations (Hill and Gauch 1980). For each site we used the mean number of singing males of each group across the 5 sampling days to relate species abundance to environmental variables. We carried out a PCA and a redundancy analysis (RDA) to investigate functional group composition and relation to environmental variables. The significance of environmental variables in explaining abundance of functional groups was tested with Monte Carlo permutation tests in a RDA in Canoco. Ordinations are not as sensitive to intercorrelated variables as a normal regression analyses, so we included most of the environmental variables measured, but removed the environmental variables that were highly correlated with other variables in the analysis.

The environmental variables that contributed to explaining the variation of functional group abundance in ordinations were further explored for each functional group in a mixed model with Poisson distributed errors using the GLIMMIX macro in SAS (Littell 2006). Instead of using a repeated design, we used the mean abundance over five sampling events, and added the number of the observation site as a random intercept. The abundance of nesting height groups was analysed only with linear models in SAS, as there were only three groups.

We analysed the individual bird species response to habitat variables with the same linear methods in Canoco as for functional group abundance. In ordinations we excluded species that were observed only once (see Appendix), so that rare species should not dominate in the ordination.

Results

Effects of moose browsing and feeding stations on total species richness and abundance

We recorded a total of 32 species of territorial birds (see Appendix). Bird species richness and abundance showed

no difference when comparing feeding stations and controls alone using ANOVA (richness $F_{1,20} = 0.15$, $P = 0.70$; abundance $F_{1,20} = 0.16$, $P = 0.69$, Fig. 1a). However, the large variation in browsing pressure on controls made it possible to analyse the effects of browsing and of feeding stations separately (Fig. 1b). The minimum adequate model for species richness included the variables birch browsing, feeding station/control, observer (grouped) and vegetation-PCA axis 2 (Table 2). Species richness decreased with increasing birch browsing, but species richness was higher at feeding stations than at controls with equally high browsing pressure (Table 3; Fig. 1b). At the control sites, species richness decreased from 7.4 (± 1.1 SE) to 4.8 (± 1.0 SE) species per site (-35%) when birch browsing increased from 10 to 95% (Fig. 1b), whilst species richness at feeding stations was 0.81 (± 1.0 SE)

species per site higher ($+17\%$) than at controls. Species richness was positively correlated with vegetation-PCA axis 2, representing a positive correlation with spruce forest or a negative correlation with lichen/pine forest. The variables that best described the abundance of territorial males included feeding station/control, birch browsing, observer and date (grouped) (Table 3). Abundance of territorial males showed the same pattern as species richness (Fig. 1c). Abundance decreased from 9.3 (± 1.1 SE) birds per site at 10% browsing pressure to 6.5 (± 1.1 SE) at 95% browsing pressure at controls (-30%), but was 0.84 (± 1.1 SE) birds per site higher ($+13\%$) at feeding stations compared to controls.

Response of functional groups to birch browsing and feeding stations

An RDA of the abundance in different functional groups selected the following variables by Monte Carlo tests (including 999 permutations): birch browsing ($F = 2.22$, $P = 0.092$), percentage cover of pine less than 3 m high ($F = 2.26$, $P = 0.092$), feeding station ($F = 2.35$, $P = 0.058$) and cutting class 2 ($F = 2.13$, $P = 0.088$), together explaining 37% of the variation in bird species composition. From interpretation of the PCA diagram, we could identify two main modes of reaction to birch browsing: seed-eaters were correlated positively with birch browsing, whilst the insect-eaters were correlated negatively with birch browsing, and mixed seed–insect eaters were in an intermediate position (Fig. 2a). There was no clear pattern between groups with different migration strategy (Fig. 2a). All functional groups seemed to be correlated negatively with cover of small pine, and strict insect eating groups were most abundant in cutting class 2 (Fig. 2a). The same patterns can be observed in the ordination of individual species (Fig. 2b).

As functional groups with a similar diet (seeds/insects) responded in similar ways to birch browsing in the ordination diagram, we grouped the bird species into larger groups of seed- or insect-eaters, but excluded mixed seed–insect feeders because of their intermediate position, and woodpeckers because of their different ecology. Then we tested for an interaction between diet (seed/insect), feeding station and birch browsing. There was a significant interaction between diet and the effects of both feeding station ($F_{1,19} = 8.31$, $P = 0.0095$) and birch browsing ($F_{1,19} = 15.36$, $P = 0.0009$) on abundance. Insect eaters decreased in abundance with increasing birch browsing, but had a higher abundance at feeding stations compared to controls, whilst seed eaters increased with increasing birch browsing and had a lower abundance at feeding stations compared to controls (Fig. 3a).

The abundance of birds in the different nesting categories responded differently to birch browsing, but not to feeding treatment ($F_{1,60} = 1.68$, $P = 0.120$). The interaction between nesting group and birch browsing

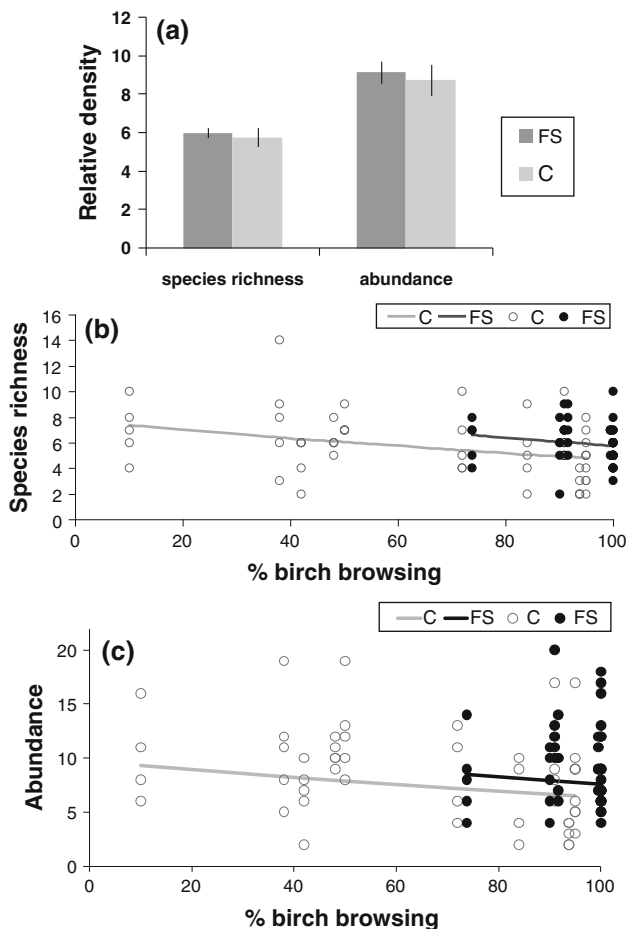


Fig. 1a–c Effects of moose browsing and supplementary feeding stations on bird species richness and abundance. **a** Comparison of bird species richness and abundance between feeding treatments (FS feeding station, C control > 1 km from feeding station). **b** Bird species richness per site in relation to birch browsing (% of twigs browsed) and feeding treatment. The predicted model line shown is standardised for effects of observer and vegetation type. **c** Bird abundance per site in relation to birch browsing (% of twigs browsed) and feeding treatment. Observations for all five sampling events are shown in **b** and **c**, although some data points are overlapping, especially for FS

Table 3 Solution for fixed effects with Poisson-distributed errors for the model with the lowest AICc for species richness (model 3 Table 2) and abundance of territorial male birds at feeding stations for moose and controls (1 km from feeding station)

Effect	Levels	Estimate	Standard error	Den <i>df</i>	<i>t</i> value	Pr > <i>t</i>
Species richness						
Intercept		2.45	0.14	18	17.40	< 0.0001
FS_C	Control	-0.21*	0.069	18	-3.03	0.007*
FS_C	Feeding station	0	–	–	–	–
Observer gr2	BBKMRO	-0.19	0.060	36	-3.09	0.004
Observer gr2	CS	-0.53	0.098	36	-5.43	< 0.0001
Observer gr2	LH	0	–	–	–	–
Birch browsing		-0.0050*	0.0013	18	-3.77	0.0014*
Vegetation pca axis 2		0.063*	0.028	18	2.22	0.039*
Abundance						
Intercept		2.50	0.15	19	16.19	< 0.0001
FS_C	Control	-0.15*	0.075	19	-2.01	0.058*
FS_C	Feeding station	0	–	–	–	–
Observer gr1	BBLH	0.57	0.059	21	9.58	< 0.0001
Observer gr1	CSKMRO	0	–	–	–	–
Date gr1	16 May–6 June	-0.29	0.067	21	-4.31	0.0003
Date gr1	7 May	0	–	–	–	–
Birch browsing		-0.0034*	0.0014	19	-2.39	0.027*

For categorical variables, one of the categories is given 0 as the reference level. The observers are grouped according to differences in detection of birds, in three groups for species richness, for abundance two groups. Date (abundance) is grouped into two groups, as significantly more birds were observed on 7 May

*Important results

was significant ($F_{3,59} = 5.03$, $P = 0.0036$). The abundance of birds nesting below browsing height and at browsing height decreased with increasing birch browsing, whilst abundance of birds nesting above browsing height increased with increasing birch browsing (Fig. 3 b).

Responses of individual bird species to feeding stations and birch browsing

Few species showed significant differences in abundance between feeding stations and controls, except the pied flycatcher (*Ficedula hypoleuca*), which had a higher abundance at feeding stations than at control sites (see Appendix, Fig. 2b). To control that the overall positive effects of feeding stations on bird abundance were not due just to this species, we ran the analysis of feeding groups and species richness again excluding the flycatcher. The interaction between feeding stations and abundance of insect/seed eaters was still significant ($F_{1,119} = 6.59$, $P = 0.019$), while the positive effect of feeding stations on species richness remained although not significant ($F_{1,18} = 4.08$, $P = 0.058$). In an RDA of abundance of all bird species, selection with Monte Carlo permutation showed that only the variables birch browsing ($F = 2.47$, $P = 0.024$) and cutting class 2 ($F = 2.04$, $P = 0.036$) contributed significantly towards explaining the variation in abundance of individual bird species. Birch browsing explained most of the variation in bird species abundance (11%), while feeding station/control explained 4% of the variation ($F = 1.31$, $P = 0.23$) once birch browsing and cutting class 2 were added to the model. *Parus major* and

Phylloscopus trochilus were common far from feeding stations, most frequent in cutting class 2, and seemed to be negatively correlated with birch browsing (Fig. 2b). The seed-eater *Carduelis spinus* was also most abundant far from feeding stations (Fig. 2b). Insect-eaters tended to be negatively correlated to birch browsing, except *Ficedula hypoleuca* and *Regulus regulus*, which may be positively correlated with birch browsing (Fig. 2b).

Discussion

Feeding stations had a net zero effect on bird species richness and abundance in accordance with scenario 2, as negative effects of moose browsing on birch were balanced by positive effects of feeding stations (Fig. 1a–c). The positive effect of feeding stations was most likely caused by positive effects of input of nutrients to the ecosystem. Different functional groups of birds showed opposite responses to browsing and nutrient input; insect-eating species responded negatively to birch browsing but positively to nutrient input at feeding stations, whereas seed-eating species responded positively to birch browsing and negatively to feeding stations. Birds nesting at or below browsing height were negatively affected by moose browsing, whereas species nesting above the browsing zone were positively affected by moose browsing.

Negative effects of heavy browsing or grazing by ungulates on abundance and species richness of birds have been documented in earlier studies (Fuller 2001; Suominen and Danell 2006), but these effects have been linked mostly to changes in vegetation structure (Allombert et al. 2005; Berger et al. 2001; DeCalesta

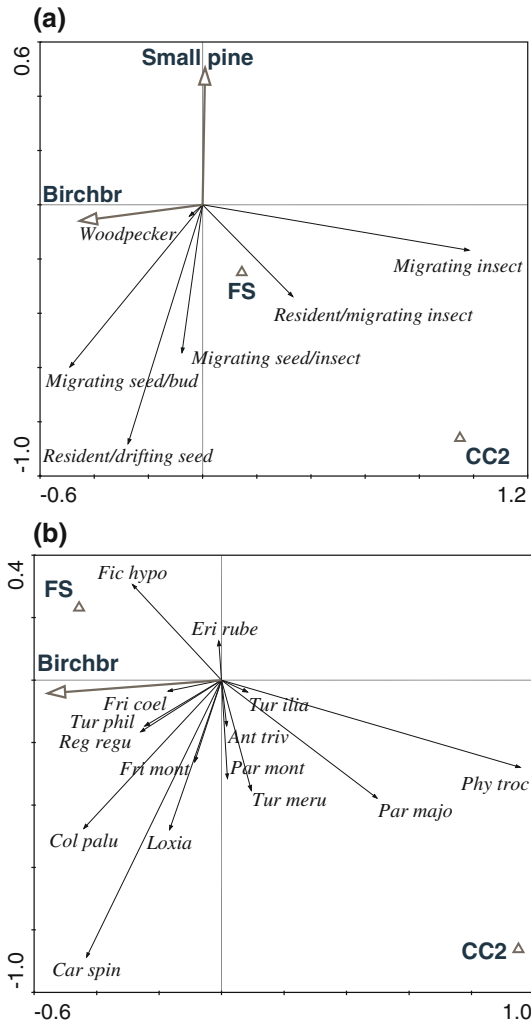


Fig. 2 Principal component analysis (PCA) of **a** functional groups and **b** individual species. The most significant environmental variables from the RDA were added according to best fit. Categorical variables are shown as *triangles*, continuous as *thick arrows*, and bird species as *thin arrows*. *CC2* Cutting class 2, *Birchbr* birch browsing (% shoots browsed), *FS* feeding station, *small pine* % cover of pine below 3 m. **a** The variables shown in the figure explained 37% of the variation in abundance of functional groups. **b** Only species with more than 20 observations are shown to ease interpretation of the figure. Feeding station was also added to **b** even though it was not significant, to see how different species relate to feeding station. The variables shown in **b** explained 24% of the variation in species abundance. For full names of bird species, see [Appendix](#)

1994; McShea and Rappole 2000) whilst our results indicate that reduced food resources for insectivorous birds may also be an important mechanism. Although heavy or long-term browsing pressure seems to have negative effects on bird diversity, low or short-term grazing pressure can, in some ecosystems, have a positive effect on bird diversity (Loe et al. 2007). The documented positive effect of nutrient input at supplementary feeding stations on bird species richness is unique to this study. Folkard and Smith (1995) showed that fertilisation in boreal forest can have positive effects

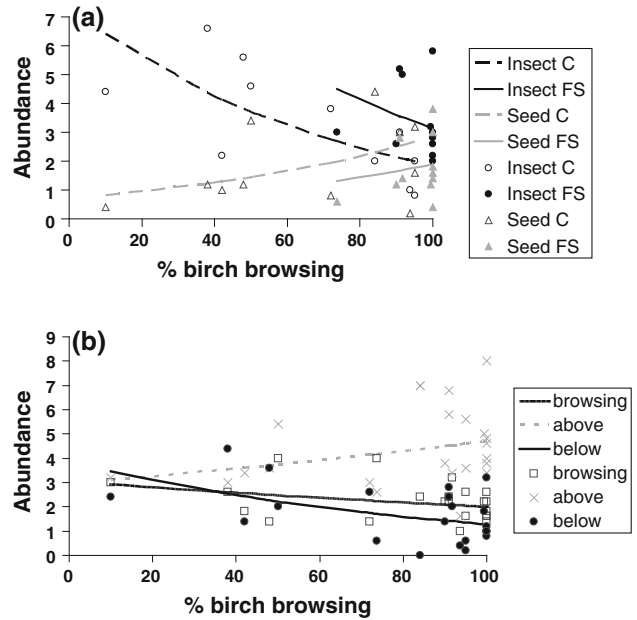


Fig. 3a,b Responses of functional groups to birch browsing and feeding stations. **a** Interaction between abundance of individuals belonging to feeding groups of birds (seed-eater or insect-eater) and the response to percentage birch browsing and feeding stations. *FS* Feeding station for moose, *C* control > 1 km from feeding station. **b** Abundance of individuals belonging to three nesting groups of birds at different degrees of birch browsing (data from *FS* and *C* are pooled). Nesting groups are; below, at and above browsing height (0.5–3 m) for moose. For both **a** and **b** the mean numbers of territorial males observed per site over 5 observation days are shown as *points*, the regression model as a *line*

on bird abundance, probably due to increased plant growth increasing arthropod availability.

We found that bird species nesting at and below respective browsing height were affected negatively by birch browsing. Earlier studies have also identified nesting height as an important factor explaining bird responses to browsing (Allombert et al. 2005; Berger et al. 2001; Casey and Hein 1983; DeCalesta 1994; McShea and Rappole 2000). For birds nesting at and below browsing height, browsing and trampling may lead to loss of nesting sites. Moose browsing changes tree structure and opens up the canopy (Mathisen et al. 2010; Persson et al. 2005a, 2007) and may increase nest predation from avian predators (Martin and Joron 2003). However, the abundance of birds nesting above browsing height was correlated positively with birch browsing.

The dominance of insect-eating birds in the bird community in this study most likely explains why the overall abundance and species richness of birds showed the same response as the insect eaters. The negative correlation between abundance of insectivorous birds and birch browsing suggests that moose browsing has a negative effect on the food resources or foraging sites for insectivorous birds, and that they choose their breeding habitat to avoid heavily browsed areas. Since many of the insectivores nest at or under browsing height, we

cannot separate the effect of birch browsing on habitat structure from that on food availability. However, the fact that feeding stations had a higher abundance of insectivorous birds than control areas with equally high browsing pressure supports that the effect on food availability was the driving factor. Furthermore the effect of feeding stations was not significant for nesting groups, suggesting an effect of feeding stations on food availability rather than habitat structure. The explanation may be that nutrient input through dung, urine and residual silage directly and/or indirectly increased the availability or quality of arthropod prey.

Previous studies have shown diverse effects of cervid browsing on abundance and diversity of different arthropod groups (Danell and Huss-Danell 1985; Riipi et al. 2005; Stewart 2001; Suominen 1999; Suominen et al. 2008), but heavy browsing is reported to have mainly negative effects (Miyashita et al. 2004; Shimazaki and Miyashita 2002; Stewart 2001; Suominen 1999; Suominen et al. 2008), especially on herbivorous insects (Suominen and Danell 2006). Moose browsing may reduce arthropod availability through reduced birch leaf biomass (Pedersen et al. 2007; Persson et al. 2007), changed chemical content (Danell and Huss-Danell 1985) or changed tree species composition (Pastor and Naiman 1992). Few studies have investigated the link between browsing, invertebrates and insectivorous birds, but Bailey and Whitham (2003) have shown experimentally that elk (*Cervus canadensis*) browsing on aspen can reduce abundance of galling sawflies, arthropod availability and foraging activity of insectivorous birds. Pedersen et al. (2007) have also suggested a link between moose browsing, invertebrate availability and breeding success in great tits (*Parus major*) in the same study area.

At feeding stations the input of nutrients from animal excreta and silage residues may favour some arthropod groups directly or via changes in plant biomass and chemistry (Stewart 2001). The mechanism may be increased arthropod availability with the increase in herbs and grasses at enriched feeding stations (Strengbom and Nordin 2008; Torgersen 2008). Changed nutrient availability and responses in the vegetation may lead to increase in body-size or abundance of some arthropod groups (Strengbom et al. 2005; Throop and Lerdau 2004). Another possibility is increase in dung-related arthropods (Rice 2010), or arthropods in silage remains. In a parallel study (K.M.M. et al. unpublished) it was observed that great tits brought back larger caterpillars to the nest boxes at feeding stations than at sites with high browsing pressure and low nutrient input.

Granivorous bird abundance was correlated positively to birch browsing, but was lower at feeding stations than at controls of similar browsing pressure. This implies that negative effects of high levels of moose browsing were stronger than any positive

effects of nutrient input at feeding stations for granivorous birds according to scenario 1, although there was no net effect of feeding treatment. The granivores were dominated by Eurasian siskins (*Carduelis spinus*) and crossbills (*Loxia* spp.), but also wood pigeons (*Columba palumbus*) and bullfinches (*Pyrrhula pyrrhula*) belong to this group. Birch seeds is an important food for siskins, and Bergström and Danell (1987) have shown that birch when subject to browsing produces fewer but heavier seeds, which might explain the positive correlation between granivorous bird abundance and birch browsing. Siskins, crossbills and wood pigeons nest above browsing height, and were probably less affected by effects of moose browsing on nesting sites, which means that the positive correlation between browsing and bird abundance can also be explained by nesting group. However, since the effect of feeding stations was not significant for nesting groups, this suggests that the mechanism behind reduced abundance at feeding stations is related to food availability rather than the availability of nesting sites.

The pied flycatcher (*Ficedula hypoleuca*) was the only bird species that had a higher abundance at feeding stations than at controls. The flycatcher prefers open areas and catches insects by air sallying (Sanz 1998; Waldbauer 1998), and may profit from more open vegetation caused by moose browsing, or an increase in arthropod prey abundance caused by the increase in dung, urine, residual silage and herbs at feeding stations. It has been suggested that deer browsing may be positive for this species in British woods (Fuller 2001). A parallel study of reproduction in flycatchers in the same area over several years also shows a preference for nest-boxes at feeding stations, a higher number of fledglings produced at feeding stations and a higher feeding frequency in bird boxes at feeding stations compared to controls (K.M.M., unpublished data). The goldcrest (*Regulus regulus*) was the other common species that did not show the same response to birch browsing as the rest of the insect-eating group. However, this species commonly nests high above browsing height (Cramp 1977), and might therefore be less affected by moose browsing.

Supplementary feeding stations may be positive for bird diversity because of positive local fertilisation effects and increasing variation in moose density on a landscape scale. However, supplementary feeding may sustain high moose population densities leading to negative effects of high browsing pressure. Effects of browsers on the ecosystem are complex and dynamic, and the mechanisms are still poorly understood, and should be further investigated using well designed experiments. Today, many bird populations inhabit forests managed for timber production, and high moose densities and intensive browsing pressure should be a concern for bird diversity conservation within

wildlife management and forestry practices. Birds can serve as indicator species of ecosystem function, and when bird diversity changes this is a sign that the ecosystem is changing. Such high moose browsing pressure as in this study is only common locally where moose concentrate on winter feeding grounds. However, densities of moose have been extraordinarily high during the last decades in Fennoscandia, as have the densities of other browsers in Europe and North-America, and changes in the ecosystems caused by these browsers have been documented. As dynamics are changing in boreal forest systems, with global warming, changes in forestry practices and the re-establishment of large predators, it is especially important to understand how large ungulate activities can have cascading effects on other animals and ecosystem processes.

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Appendix: Bird species observations and functional group classification

See Table 4.

Table 4 Total number of observations of bird species observed over 5 observation days in point counts of singing males at 11 feeding stations (FS) for moose and 11 controls (C) > 1 km from feeding station in Stor-Elvdal municipality, Hedmark County, Norway

Migratory strategy	Diet	Nest height	English name	Latin name	Mean FS ± SE	Mean C ± SE	Total observations
Migrating	Insects	Under br	Willow warbler	<i>Phylloscopus trochilus</i>	0.89 ± 0.36	1.27 ± 0.36	119
Migrating	Insects	Under br	Tree pipit	<i>Anthus trivialis</i>	0.58 ± 0.11	0.36 ± 0.11	52
Migrating	Insects	At br	Pied flycatcher	<i>Ficedula hypoleuca</i>	0.45 ± 0.07	0.13 ± 0.07	32
Migrating	Insects	At br	Dunnock	<i>Prunella modularis</i>	0.09 ± 0.06	0.13 ± 0.06	12
Migrating	Insects	Other	Cuckoo	<i>Cuculus canorus</i>	0.09 ± 0.05	0.07 ± 0.05	9
Migrating	Insects	Under br	Chiffchaff	<i>Phylloscopus collybita</i>	0.02 ± 0.06	0.09 ± 0.06	6
Migrating	Insects	Other	Wren	<i>Troglodytes troglodytes</i>	0.07 ± 0.02	0.04 ± 0.02	6
Migrating	Insects	At br	Garden warbler	<i>Sylvia borin</i>	0.02 ± 0.04	0.09 ± 0.04	6
Migrating	Insects	At br	Lesser whitethroat	<i>Sylvia curruca</i>	0.07 ± 0.02	0.02 ± 0.02	5
Migrating	Insects	At br	Blackcap	<i>Sylvia atricapilla</i>	0.02 ± 0.04	0.04 ± 0.04	3
Migrating	Insects	Under br	Whinchat	<i>Saxicola rubetra</i>	0.02 ± 0.00	0.00 ± 0.00	1
Migrating	Insects	At br	Common redstart	<i>Phoenicurus phoenicurus</i>	0.02 ± 0.00	0.00 ± 0.00	1
Migrating	Seeds and buds	Over br	Common wood pigeon	<i>Columba palumbus</i>	0.24 ± 0.09	0.29 ± 0.09	29
Migrating	Seeds and insects	Over br	Chaffinch	<i>Fringilla coelebs</i>	2.09 ± 0.09	1.76 ± 0.09	212
Migrating	Seeds and insects	At br	Robin	<i>Erithacus rubecula</i>	0.47 ± 0.10	0.56 ± 0.10	57
Migrating	Seeds and insects	At br	Song thrush	<i>Turdus philomelos</i>	0.56 ± 0.12	0.47 ± 0.12	57
Migrating	Seeds and insects	Over br	Brambling	<i>Fringilla montifringilla</i>	0.36 ± 0.08	0.25 ± 0.08	34
Migrating	Seeds and insects	At br	Redwing	<i>Turdus iliacus</i>	0.22 ± 0.08	0.24 ± 0.08	25
Migrating	Seeds and insects	At br	Blackbird	<i>Turdus merula</i>	0.16 ± 0.05	0.22 ± 0.05	21
Migrating	Seeds and insects	Over br	Mistle thrush	<i>Turdus viscivorus</i>	0.02 ± 0.00	0.00 ± 0.00	1
Resident	Woodpecker	Over br	Great spotted woodpecker	<i>Dendrocopos major</i>	0.04 ± 0.04	0.05 ± 0.04	5
Resident	Woodpecker	Over br	Black woodpecker	<i>Dryocopus martius</i>	0.05 ± 0.02	0.04 ± 0.02	5
Resident/drifting	Seeds	Over br	Eurasian siskin	<i>Carduelis spinus</i>	1.29 ± 0.29	1.33 ± 0.29	144
Resident/drifting	Seeds	Over br	Crossbill	<i>Loxia spp.</i>	0.20 ± 0.12	0.18 ± 0.12	21
Resident/drifting	Seeds	At br	Common bullfinch	<i>Pyrrhula pyrrhula</i>	0.02 ± 0.04	0.05 ± 0.04	4
Resident/migrating	Insects	Other	Great tit	<i>Parus major</i>	0.47 ± 0.14	0.47 ± 0.14	52
Resident/migrating	Insects	Over br	Goldcrest	<i>Regulus regulus</i>	0.27 ± 0.08	0.20 ± 0.08	26
Resident/migrating	Insects	At br	Willow tit	<i>Parus montanus</i>	0.15 ± 0.10	0.24 ± 0.10	21
Resident/migrating	Insects	Other	Coal tit	<i>Parus ater</i>	0.09 ± 0.02	0.04 ± 0.02	7
Resident/migrating	Insects	Under br	Yellowhammer	<i>Emberiza citrinella</i>	0.02 ± 0.05	0.09 ± 0.05	6
Resident/migrating	Insects	At br	Crested tit	<i>Parus cristatus</i>	0.04 ± 0.00	0.00 ± 0.00	2
Resident/migrating	Insects	Other	Blue tit	<i>Parus caeruleus</i>	0.02 ± 0.00	0.00 ± 0.00	1

Species are grouped into functional groups after migration strategy and diet in the nesting period. Species are defined as nesting under, at or over browsing (br) height (0.5–3 m) for moose

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